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Detection of earthworm prey by Ruff *Philomachus pugnax*

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Ruff *Philomachus pugnax* staging in the Netherlands forage in agricultural grasslands, where they mainly eat earthworms (Lumbricidae). Food intake and the surface availability of earthworms were studied in dairy farmland of southwest Friesland in March–April 2011. Daily changes in earthworm availability were quantified by counting visible earthworms. No earthworms were seen on the surface during daytime, but their numbers sharply increased after sunset and remained high during the night. Nevertheless, intake rates of individual Ruff in different grasslands measured during daytime showed the typical Holling type II functional response relationship with the surfacing earthworm densities measured at night. Radiotagging of Ruff in spring 2007 revealed that most, if not all, feeding occurs during the day, with the Ruff assembling at shoreline roosts at night. This raises the question of why Ruff do not feed at night, if prey can be caught more easily than during daytime. In March–May 2013 we experimentally examined the visual and auditory sensory modalities used by Ruff to find and capture earthworms. Five males were kept in an indoor aviary and we recorded them individually foraging on trays with 10 earthworms mixed with soil under various standardized light and white noise conditions. The number of earthworms discovered and eaten by Ruff increased with light level, but only when white noise was played, suggesting that although they can detect earthworms by sight, Ruff also use auditory cues. We suggest that although surfacing numbers of earthworms are highest during the night, diurnal intake rates are probably sufficient to avoid nocturnal foraging on a resource that is more available but perhaps less detectable at that time.

Keywords: foraging, Lumbricidae, predator–prey interactions, sensory ecology.

To understand the interactions of predator and prey, it is necessary to know about the sensory ecology of both actors, i.e. how a predator detects and catches its prey and how the availability of the prey changes over time (Zwarts & Wanink 1993, Barbosa & Castellanos 2005, Piersma 2011). Earthworms (Lumbricidae) are soil-dwelling organisms that are important food for a wide variety of predators (MacDonald 1983). Earthworms can be caught by probing the soil surface (e.g. the long-billed sandpipers; Burton 1974) or digging through the soil (e.g. Moles *Talpa europaea*; Raw 1966). However, as Darwin (1881) observed, earthworms also come to the soil surface themselves and then are fed upon by visual hunters, including birds (e.g. Golden Plovers *Pluvialis apricaria*: Bengtson *et al.* 1978; Blackbirds *Turdus merula*: Chamberlain *et al.* 1999; reptiles and amphibians: Hamilton 1951, MacDonald 1983).

A migratory sandpiper, the Ruff *Philomachus pugnax*, is virtually extinct as a breeding species in the Netherlands (Boele *et al.* 2016), but still stages there during the migration period (Jukema *et al.*

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2001, Verkuil *et al.* 2010), albeit in greatly diminished numbers (Schmaltz *et al.* 2015). Ruff use freshwater wetlands and agricultural grasslands, but deterioration of these habitats may have caused declining numbers of staging birds in the Netherlands and a shift towards a more easterly migration route (Verkuil *et al.* 2012). Ruff are opportunistic feeders and can feed on plant materials as well as invertebrates (Ezealor & Giles 1997, Baccetti *et al.* 1998). In the Netherlands, Ruff primarily use moist grasslands for feeding (Verkuil & de Goeij 2003, Schmaltz *et al.* 2016), and their main prey then are earthworms (van Rhijn 1991), sometimes supplemented by leatherjackets (larvae of Tipulidae) (Beintema *et al.* 1995). When earthworms become less available due to desiccation of the soil and with increasing sward height, Ruff can switch to eating insects by picking them from the foliage if these become available on warm spring days (Verkuil & de Goeij 2003, Schmaltz *et al.* 2016).

How Ruff detect the earthworm prey remains unclear. Routinely, deep probing of the soil has been observed (Verkuil & de Goeij 2003, Krupa *et al.* 2009), which suggests that they can use tactile foraging strategies or that they merely chase retreating prey they had detected in other ways. Indeed, van Rhijn (1991) and Barbosa (1995) identify Ruff as a tactile forager. Hoerschelmann (1970), on the other hand, suggests that the Ruff is a typical visual forager, on the basis of the shape and structure of the bill. Ruff have relatively short bills (30–31 mm for females, 34–35 mm for males; Meissner & Ziêcik 2005), and the tip of a Ruff's bill contains fewer sensory cells than that of more tactile foraging wader species (Ballmann 2004). Nevertheless, Thomas *et al.* (2006) stated that Ruff use a mixture of both techniques with no bias towards visual or tactile foraging.

Earthworms may come to the surface during the night (Butt *et al.* 2003) and can then be detected by sight under low illumination. Given their nocturnal surfacing behaviour, at least for visual foragers with good night vision, it would be beneficial to forage nocturnally (McNeil & Rodríguez S. 1996, Lourenço *et al.* 2008). This seems to be the case for Golden Plovers, which have relatively large eyes and probably also a high rod-to-cone ratio for good night vision (Rojas *et al.* 1999, Martin & Piersma 2009). Ruff, however, have relatively small eyes (Thomas *et al.* 2006). Surprisingly, Cramp and Simmons (1983) state that Ruff mainly forage during twilight and at night. It is possible that, depending on ecological context, they switch from being visual hunters by day to tactile feeders by night, as is observed in other shorebird species (Mouritsen 1994, Burton & Armitage 2005). At night, they could also use auditory cues to locate a digging earthworm, as is done by thrushes (Turdidae) during daytime (Montgomerie & Weatherhead 1997) and possibly also by Golden Plovers (Lange 1968).

On the basis of these conflicting statements, we predicted that Ruff use visual cues to catch earthworms, but might switch to using auditory cues in darkness. We used field observations of earthworm-eating Ruff to quantify feeding performance during the day in relation to available prey densities at night, and used radiotelemetry data to establish whether Ruff are indeed diurnal foragers at our study site. We then performed a controlled indoor experiment to examine the capacity of Ruff to use visual and auditory cues in the detection of earthworms.

METHODS

The predator and its prey: field observations

All fieldwork was conducted in southwest Friesland, the Netherlands (within a radius of about 10 km of 52°55′N, 5°26′E). In this region the total land area consists mainly of grasslands used for dairy farming (Groen *et al.* 2012). These grasslands are used by Ruff to forage and the numerous lakes and shorelines are used as roosting sites (Verkuil & de Goeij 2003, Schmaltz *et al.* 2016).

From 21 March to 15 April 2011, foraging Ruff were studied in relation to the earthworm conditions in selected fields. The fields were selected on the basis of the presence of flocks of Ruff (with numbers ranging between 40 and 450 individuals). On 12 different fields (all between 2 and 6.5 ha and all used for dairy farming and with a loamy clay soil), between 6 and 11 different birds each were observed between sunrise and sunset. Bird observations involved the counting of numbers of foraging birds and the scoring of individual prey intake rates. Intake rate was defined as number of eaten earthworms per minute. Intake rates of a focal individual were scored for 5 min using a 20–60× magnification telescope. Intake rates were scored for exactly 100 different Ruff. Although

earthworms could be positively identified as prey (their colour, size and behaviour), not every prey item or swallowing action could be identified and therefore only definitely consumed earthworms were counted. This leads to underestimation of the intake rate. Field observations were stopped when Ruff switched to eating insects. Ruff feeding on insects can clearly be distinguished from earthworm-eating Ruff as their pecking at insects on the foliage results in a very different posture, head movements and gait.

Visual counts of earthworms were made a day later in the fields where the intake rate observations were made. Surfacing earthworms were counted by lying prone on a robust and simple cart which was gently pushed forward by foot. This cart provided the observer with a good view of the soil (head *c.* 40 cm above surface) and it created little vibration. Visual counts consisted of counting the surfacing earthworms along two transects of 75 m per grassland. Every earthworm within 50 cm of the central transect line was counted. In this way, about 75 m^2 was covered per sampling event. One transect took about 45 min to complete. The counts were repeated five times throughout the day at 07:00, 10:00, 14:00, 18:00 and 21:00 h CEST, with the second transect starting an hour after the first. Sunrise during the observation period was between 06:22 and 07:08 h CEST and sunset between 20:08 and 20:44 h CEST. Light intensity during observations was not measured. A head torch (160 Lumens) and a hand-held counter were used to see and count the earthworms after sunset. Earthworms sometimes reacted to the bright light of the head torch, but they retreated into the soil after only 1–3 s (J.O.). As we show below, we never saw any surfacing earthworm during the day and therefore we correlated our measurements of intake rate by Ruff with nocturnal surface availability of visual counts performed after sunset (21:00 and 22:00 h CEST). We used the Type II response model of Holling (1959) to describe the relationship in a biologically sensible way (Duijns *et al.* 2015).

In spring 2007, 46 male Ruff were caught and applied with 1.8 g radio-transmitters (BD-2 transmitters; Holohil Systems Ltd, Carp, ON, Canada). This was part of a study determining departure dates on migration (Verkuil *et al.* 2010). Receiver stations were placed at nine roosts throughout the study area (for a map with the roosts locations, see Schmaltz *et al.* 2016). Data were collected between 25 March and 8 May 2007. As the transmitters had a detection range of about 500 m, the receiver stations could potentially also record nearby foraging birds. To be certain that birds on a roost were not foraging, we only used data of the four offshore roosts where Ruff cannot forage (for locations see the map in Verkuil *et al.* 2010; the roosts used in this paper are: Bocht fan Molkwar, Makkumer Noardwaard, Makkumer Súdwaard and Mokkebank). This selection decreased the number of radiotagged birds to 19. For the whole time period, we calculated the hourly percentage of birds present on a roost from the total number of birds present per hour and the maximum number of birds that were observed at the roosts.

Sensory capacity: prey detection trials

Five male Ruff were caught in southwest Friesland by standard *wilsternetter* procedures (for description and routines, see Rogers & Piersma 2005). To prevent sexual interactions during the experiments, we selected only adult males. After capture, the birds were individually colour-ringed and transported to an indoor aviary of 2 × 2.6 × 4 m (width, height, depth) at the Groningen Institute for Evolutionary Life Sciences in Groningen, the Netherlands, 100 km from the site of capture. To acclimatize the birds to human presence and to reduce the effects of sudden human sounds, a radio station with human voices and music was broadcast continuously. As male Ruff became competitive in spring, wooden dividers were placed in the aviary so that the birds could avoid each other; still, they could move freely through the room and engage in social interactions. During the off-trial days, Ruff were provided *ad libitum* with commercially obtained live mealworms (*Tenebrio molitor* larvae), earthworms (*Dendrobaena veneta* and *Eisenia fetida*) and fresh water.

The prey detection trials started when the birds seemed to have fully adjusted to captivity conditions, 2 weeks after capture. Experimental trials were carried out in the mornings. To motivate Ruff to feed during a trial, birds were deprived of food for 12 h before the start of each trial. Fresh water remained available *ad libitum*. On an experiment day, all birds were caught simultaneously, kept in dark boxes and randomly assigned a sequence number. Trials were carried out in the same aviary in which the Ruff were housed.

Thereafter, Ruff were placed in a small cage (width = 0.8, height = 0.4, depth = 0.4 m), which was divided in two equally sized compartments using a wooden baffle. While the ground layer present in the left side was the same as in the cage (wooden chips) and did not contain prey items, the right side was covered with a shallow layer of 1 cm clean potting soil (ingredients: 70% peat, 20% compost, 10% of an unknown fertilizer) and contained 10 earthworms (length = 50 mm), which were placed in the compartment 10 min before a trial, enabling them to bury themselves in soil and show more or less natural behaviour, but not allowing them to create burrows or casts that might help Ruff in finding them in the field. We chose to use a shallow depth of only 1 cm to be sure that the earthworms presented to the birds in every trial were more or less equally available. Only *E. fetida* earthworms were used in the experiment, as *D. veneta* actively jumps upon being touched, a behaviour that could probably make them more available than the more timid earthworm species encountered in the field (J. Onrust unpubl. obs.). After each trial the soil was removed and the number of earthworms left over was scored. Each trial was started with a new set of earthworms.

During a trial, a bird was first placed in the left side of the cage under experimental light and noise conditions. After a habituation period of 5 min we removed the wooden baffle. The bird was then able to feed for 15 min in the experimental compartment. However, full adaptation to darkness often takes about an hour in most animals (Martin 1990, Dusenbery 1992). Therefore, the visual sensitivity of the Ruff under dark conditions was probably not optimal in this experiment. However, the birds were kept for 20–100 min in dark boxes prior to the trials.

A full factorial design with the two factors light and noise was designed to examine the effects of either visual cues or auditory cues (Table 1). In addition, in Treatment 1 all cues were available and in Treatment 6 both types of cues were absent. Treatments were repeated twice for each individual. Treatments were randomly assigned to the birds following the throw of a die. Visual cues were reduced by decreasing the amount of available light; Ruff were allowed to forage under light conditions of 1000, 0.01 and 0 Lux, which correspond to daylight, twilight and complete darkness (Dusenbery 1992).

Table 1. Overview of the different experimental treatments during tests to examine the visual and auditory sensory modalities used by Ruff to find and capture earthworms.

Treatment	Background noise	Amount of light	Light level (lux)
1	Silence	Daylight	1000
2	White noise	Daylight	1000
3	Silence	Twilight	0.01
4	White noise	Twilight	0.01
5	Silence	Complete darkness	0
6	White noise	Complete darkness	0

To exclude auditory cues, we followed Montgomerie and Weatherhead (1997) and Cunningham *et al.* (2010), and used white noise to mask any sounds made by earthworms moving in the soil. White noise was generated using two speakers (output 100–18 000 Hz) placed on either side of the compartment. The sound level used to generate the white noise was 61 dB. As Ruff did not always consume every prey item they found, we recorded all trials on video (Sony Handycam HDR-SR12E with infrared function) with an extra infrared illuminator (wavelength 850 nm, range 30 m). The camera and illuminator did not create any visible light.

Videos were analysed in Windows Media Player (Windows 10). As we were primarily interested in whether Ruff were able to find earthworms, we noted the number of worms found and eaten (denoted W_{f+e}). The results were analysed in R version 3.1.2 (R Development Core Team 2014) using generalized linear mixed models with each bird (BirdID) representing a random intercept. The response variable was W_{f+e} and the explanatory variables were light and noise levels, both categorical. To control for a learning effect between the first and second repetition, we also added repetition as a variable. The package lsmeans was used for a *post hoc* analysis (Lenth 2016).

RESULTS

Field observations

The intake rate of Ruff showed a slight increase around noon ($F_{2,97} = 3.58$, $R^2 = 0.069$, $P = 0.032$, $n = 100$; Fig. 1a). During 28 h of 'carting', covering 0.21 ha of grassland, not a single surfacing earthworm was observed during daytime (Fig. 1b). Earthworms appeared on the surface only after

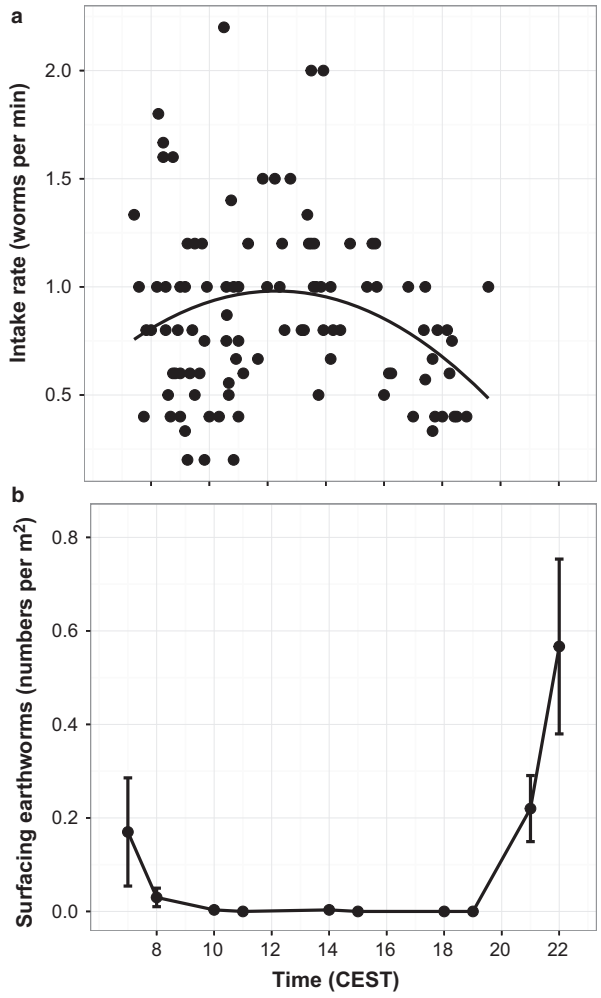

Figure 1. (a) Intake rate of Ruff feeding on earthworms is highest around noon and (b) earthworms only come to the surface during the night. Each point in (a) is an individual observation. Means and se of 12 different grasslands are shown in (b).

sunset. However, when plotted per field, the average intake rate of foraging Ruff during the day was a function of the densities of surfacing earthworms measured in darkness (the average of transects at 21:00 + 22:00 h CEST), showing the positive but steadily flattening relationship typical of a Holling type II functional response (Fig. 2, Holling 1959).

At any time of the night, 90–100% of the 19 birds were present at the roost (Fig. 3). By 08:00 h more than 90% of the birds had left the roosts and by noon about 60% were back at the roost for a daytime rest (Schmaltz *et al.* 2016, Fig. 3). Around 16:00–17:00 h, 80% of birds had left the roost again, but at twilight the majority had returned (Fig. 3).

Prey detection trials

The prey detection trials showed that prey intake under daylight was similar at the two noise levels, but in twilight and darkness, earthworms were found and eaten more in the absence of white noise (Fig. 4, Table 2). This indicates that Ruff use auditory cues to find earthworms in twilight and darkness. A *post hoc* analysis revealed, however, that only the darkness treatment with white noise was significantly different from the two daylight treatments, and twilight with white noise was significantly different from daylight without white noise (Fig. 4). As indicated by an absence of a difference between the first and second repetition of a treatment, there was no significant effect of learning (Table 2).

DISCUSSION

To explain how animals maximize their intake rate, we must consider how animals find their prey and sense the availability of prey in the field (MacArthur & Pianka 1966, Piersma 2011). We predicted that Ruff use visual cues to detect and catch earthworms in grasslands, but can switch to using auditory cues at night when food availability is highest in terms of surfacing earthworms (Fig. 1b). However, Ruff still found earthworms during daytime when human observers could not (Fig. 1), and radiotagged Ruff did not forage during the night (Fig. 3). This was unexpected, as we found the expected Holling type II functional response relationship between intake rate measured during daytime and earthworm availability measured at night (Fig. 2). This suggests that earthworms, of which some species surface during the night (Baldwin 1917), remain close to the surface during the day, so that nocturnal measurements of their surface abundance are closely correlated with their daytime availability. For example, Ruff can see parts of the earthworm, use other visual cues such as fresh earthworm casts or, indeed, hear them move. Thus, the most accurate method for measuring earthworm availability for this species should be based on the counting of visible earthworms but also on locating invisible earthworms based on the sound they produce.

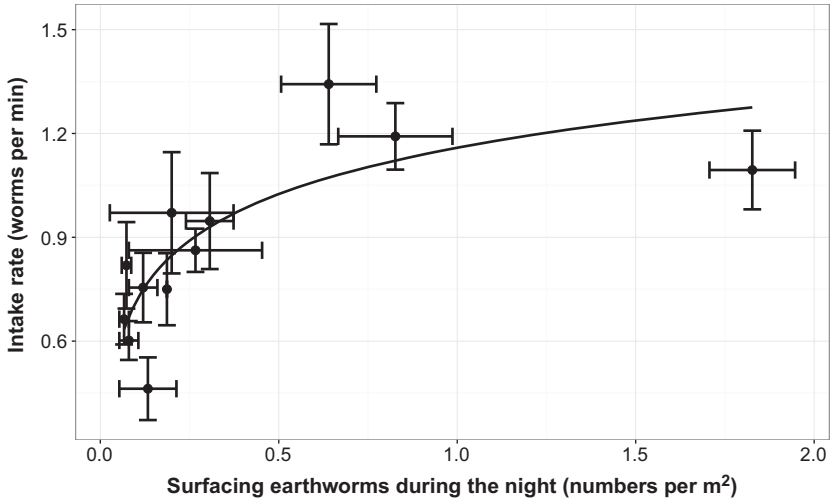

Figure 2. Intake rate on earthworms by Ruff during daytime shows a Holling type II functional response with the number of available earthworms during the night. Each point represents the average intake rate of 6–11 Ruff and the average number of earthworms counted in each of 12 fields. The equation for the fitted curve: intake rate = 1.1556 + 0.1903 (ln earthworm availability), R^2 = 0.619, P = 0.002.

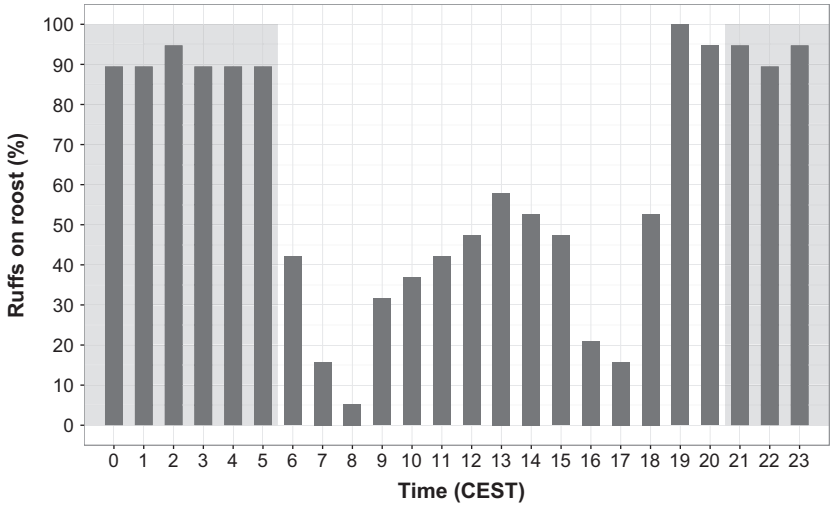

Figure 3. Ruff roost during the night and around noon. Each bar represents the hourly percentage of 19 Ruff that were present on four offshore roosts in Lake IJsselmeer, Friesland, between 28 March and 8 May 2007. Shaded areas represent the night (20:30–05:30 h CEST).

The prey detection trials with five birds and two replicates per treatment indicated that Ruff can discover earthworms in twilight and even in total darkness, with a suggestion that white noise reduces performance. This indicates that Ruff find earthworms mainly on the basis of visual and auditory cues, but in principle could also modulate the use of these cues under different light conditions. Such switches between foraging strategies in the day and night have been described previously for several different shorebirds (Hulscher 1976, Robert & McNeil 1989). In the present case, it would be mostly a switch from visual feeding during the day to tactile feeding at night, previously suggested by van Rhijn (1991), Barbosa (1995) and Thomas *et al.* (2006). However, these studies were based on observations under field conditions, whereas we forced birds to forage in the absence or presence of cues that

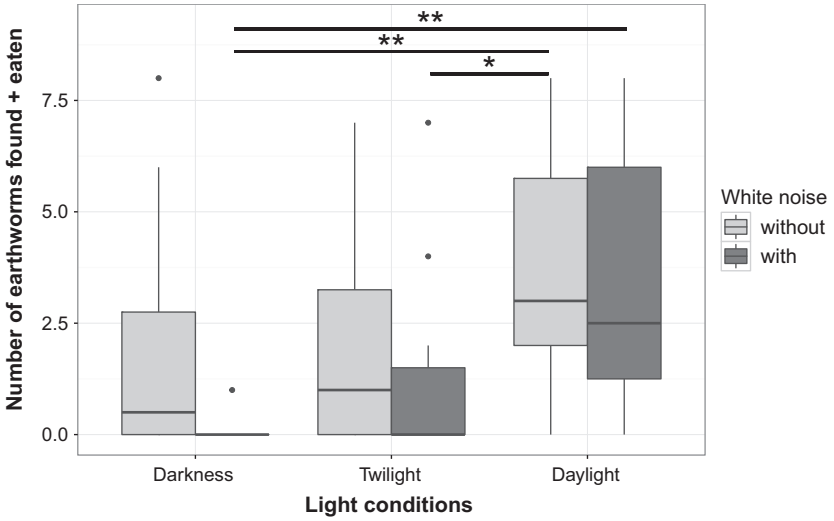

Figure 4. Results of the prey detection trials. Boxplots represent the data of five captive male Ruff under three light conditions (darkness, twilight and daylight, which correspond to 0, 0.01 and 1000 Lux, respectively) and with or without white noise. Per bird, all treatments were repeated twice. Significant differences between treatments are indicated with an asterisk (*$P \leq 0.05$).

Table 2. Coefficient estimates β, standard errors, se (β), associated Wald's *z*-score (= β/se(β)) and significance level *P* for all predictors in the analysis derived from a generalized linear mixed model (GLMM) with number of earthworms found and eaten as the response variable and light conditions and white noise (Y/N) as explanatory variables (fixed effects). Bird identity is fitted as a random effect. Reference level for white noise was 'no noise', for light levels it was darkness, and for the interaction terms it was no noise*darkness.

Predictor	Coef. β	se (β)	*z*-value	*P*-value
Intercept	−0.140	0.651	−0.214	0.830
Repetition	0.189	0.271	0.697	0.486
White noise	−2.906	1.081	−2.689	0.007
Twilight	0.067	0.458	0.146	0.884
Daylight	0.903	0.428	2.109	0.035
White noise*Twilight	2.362	1.191	1.984	0.047
White noise*Daylight	2.702	1.144	2.361	0.018

limited them to using either a visual or an auditory strategy. Even though our initial experimental setup was not designed to test whether Ruff use tactile cues, Ruff were not able to find worms when both visual and auditory cues were eliminated (treatment 6). This suggests that we successfully eliminated all the cues used by Ruff. Although the difference between white noise in darkness and no white noise is not significant, if Ruff primarily use tactile cues to find prey, they should also have found earthworms in darkness when white noise was played (Fig. 4).

Over the last two decades the numbers of staging Ruff have declined considerably in the Netherlands (Jukema *et al.* 2001, Verkuil *et al.* 2010, 2012). Agricultural intensification has resulted in grasslands that are less attractive for feeding. Although earthworms can profit from higher manure input (Hansen & Engelstad 1999), earthworm availability for Ruff might have declined because of generally drier conditions (Ausden & Bolton 2012). To avoid the drought, earthworms in drained grasslands retreat deeper into the soil (Gerard 1967). Furthermore, tipulid larvae are also susceptible to desiccation and avoid drained grasslands (Pritchard 1983, Carroll *et al.* 2011). This may provide part of the reason why Verhulst *et al.* (2007) found a positive relationship between groundwater level and meadow bird numbers and prey density. High groundwater levels also have a positive effect on the penetrability of the soil for a bird's bill, making it easier to catch earthworms (Green *et al.* 1990, Duckworth *et al.* 2010, Ausden & Bolton 2012).

In staging areas, food conditions need to be sufficient to allow migrants to gain the fuel stores for onward migration and breeding (Piersma & Baker 2000). Biometric data of Ruff that were caught as part of a long-term study monitoring the population of Ruff staging in southwest Friesland (Hooijmeijer 2007) indicated that the fuelling rates of male Ruff declined between 2001 and 2008

(Verkuil *et al.* 2012) and that birds may have had lower departure masses in recent years (L.E. Schmaltz, unpubl. data). Verkuil *et al.* (2012) argues that this is caused by a loss of moist grasslands. Indeed, the distribution in recent years of the remaining staging Ruff also hints at the importance of wet grasslands (Schmaltz *et al.* 2016).

According to McNeil *et al.* (1992), shorebirds forage at night to meet their daily energy requirements (i.e. supplementary hypothesis), or because food conditions at night are better and predation risk is lower (i.e. preference hypothesis). After sunset, food conditions for Ruff should be better, as earthworms start to surface then (Fig. 1b). Ruff can still find earthworms in darkness, probably by hearing. However, our data showed that Ruff are not nocturnally active and therefore rarely make use of auditory cues to exploit an abundant resource during the night (Fig. 4). During their migratory staging in southwest Friesland, Ruff, therefore, rarely if ever forage nocturnally. This implies that food conditions during the daytime feeding are sufficient.

In conclusion, a combination of field and experimental indoor observations on the relationships between Ruff and earthworms indicated that although we measured only surfacing earthworms during the night, Ruff predominantly fed during the day. We propose that they use indirect visual and auditory cues to detect earthworms that are already close to the surface.

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